Effects of young *Artemisia rothrockii* shrubs on soil moisture, soil nitrogen cycling, and resident herbs

Darrouzet-Nardi, Anthony[1,2*]; D'Antonio, Carla M.[1,3] & Berlow, Eric L.[1,4]

[1]*Department of Integrative Biology, University of California, Berkeley, Berkeley, CA 94720-3140 USA;*
[2]*Present address: Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309-0334 USA;* [3]*Present address: Department of Environmental Studies, University of California, Santa Barbara, Santa Barbara, CA 93106 USA;* [4]*Present address: Sierra Nevada Research Institute, Wawona Station, Yosemite National Park, CA 95389 USA;* *Corresponding author; E-mail anthony@darrouzet-nardi.net*

Abstract

Questions: How do young sagebrush shrubs (*Artemisia rothrockii*, *Asteraceae*) affect soil moisture availability? How do young sagebrush shrubs affect soil nitrogen cycling? How does the resident herb community respond to shrub removal in the early stages of sagebrush encroachment?

Location: Mulkey and Bullfrog Meadows on the Kern Plateau in the Golden Trout Wilderness, Sierra Nevada Mountains, Inyo National Forest, Inyo County, California, USA.

Methods: We removed young encroaching sagebrush shrubs from 3.5 m × 3.5 m plots and compared soil moisture, net mineralization, net nitrification, and herb cover with paired control plots over four growing seasons.

Results: On average throughout the experiment, the difference between removal plots and control plots in soil moisture was small. Removal plots were wetter by $1.3 \pm 2.0\%$ at 0-30 cm depth, $2.1 \pm 3.1\%$ at 30-60 cm depth and $3.1 \pm 5.8\%$ at 60-90 cm depth. By contrast, after four years, net mineralization was $32 \pm 26\%$ (mean ± 95% CI) lower in sagebrush removal plots, suggesting that sagebrush encroachment increases rates of N-cycling. Total herb cover was $13.0 \pm 6.4\%$ (mean ± 95% CI) higher in plots where young sagebrush shrubs were removed. This difference in cover appeared during the first season in which sagebrush shrubs were removed.

Conclusions: Our results suggest that while young sagebrush shrubs do not contribute substantially to meadow drying, they alter N cycling rates, and may indirectly increase the rate of their own encroachment by competitively reducing resident herbs.

Keywords: Groundwater decline; Nutrient cycling; Positive feedback; Stream incision; Water relations.

Introduction

Woody plant encroachment into grassland and other types of vegetation change are often accompanied by changes in ecosystem functions such as hydrologic cycling, soil nutrient cycling, and disturbance regimes (D'Antonio 2000; Ehrenfeld 2003; Levine et al. 2003). Such changes have been hypothesized to be accompanied by positive feedbacks that reinforce the altered state (e.g. Suding et al. 2004). Since changes to ecosystem function may take many years to develop, the effects of woody plant encroachment are typically inferred by examining the aftermath of encroachment through surveys of colonized and uncolonized areas or by removing stands of well-established adult woody plants (e.g., Köchy & Wilson 2000; Hibbard et al. 2001; Huenneke et al. 2002). In a recent review of the effects of plant invaders on soil nutrient cycling – many of which were encroaching trees or shrubs – Ehrenfeld (2003) noted that of 79 studies reviewed, very few provided information about plant densities or time since invasion or encroachment, making it difficult to evaluate the rate at which changes develop. To work toward filling this knowledge gap, we examined ecosystem changes during the early recruitment and growth phase of a woody plant species that is colonizing a riparian meadow ecosystem in the Sierra Nevada Mountains of California, USA.

Meadows in the southeastern Sierra Nevada that have historically been dominated by graminoids and forbs have been colonized by the sagebrush shrub *Artemisia rothrockii*, *Asteraceae* (Berlow et al. 2002). This encroachment is part of a regional phenomenon in which riparian meadows in the semi-arid American West have undergone conversion to shrub dominance following groundwater decline (Stromberg et al. 1996; Chambers & Linnerooth 2001; Wright & Chambers 2002). Although *A. rothrockii* is native to Sierra Nevada meadows (Shultz 1983), it was historically restricted to the dry meadow edges (Bauer et al. 2002). Sagebrush

encroachment began in the early 1900s following heavy livestock grazing (e.g. Muir 1911), stream incision, and groundwater decline (Dull 1999). Repeat aerial photographs and analysis of sagebrush growth rings show that sagebrush encroachment continues today, even in places with no further stream incision (Bauer et al. 2002; Swartz 2004). Between 1994 and 2001, sagebrush colonized ca. 10% of Mulkey Meadow, one of the meadows examined in this study (Swartz 2004). Due to this rapid encroachment rate and the demonstrated effects of adult shrubs on ecosystem function in our system (Berlow et al. 2003), we hypothesized that sagebrush might be having substantial effects on ecosystem function even at this early stage.

Rapid changes to ecosystem function that occur during the early stages of an invasion have several important implications. First, since sagebrush relies on the disturbance of dense mats of herbs before being able to establish in the wetter parts of the meadow (Berlow et al. 2002), a reduction in herb cover via competition for soil moisture or nutrients by young shrubs might create a positive feedback to the encroachment rate. Likewise, a redistribution of nutrients with invasion might reinforce altered conditions for herb growth. Second, changes in ecosystem function that are caused by sagebrush encroachment might potentially affect our ability to restore these meadows to a pre-sagebrush state. Given these implications, this study was designed to address three questions about changes in ecosystem function during the early stages of sagebrush encroachment: 1. How do young sagebrush shrubs affect soil moisture availability? 2. How do young sagebrush shrubs affect soil nitrogen cycling? 3. How does the resident herb community respond to shrub removal in the early stages of sagebrush encroachment?

Methods

Study site

Our study took place in two meadows, Mulkey Meadow (36°24' N, 118°12' W, 2750 m a.s.l., 2.9 km^2) and its tributary, Bullfrog Meadow (36°24' N, 118°13' W, 2750 m 0.55 km^2, Fig. 1) in the Sierra Nevada of California. Mulkey and Bullfrog Meadows receive 500-700 mm precipitation per year (Anon. 2004a). Of this, 70 mm falls in summer rainstorms; the rest is in snow (Anon. 2004a). During snowmelt, soils near the active channel are saturated with water, and the water table gets deeper toward the meadow edges. Kern Plateau meadow soils are sandy entisols with little horizonation except for occasional layers of buried peat. Soils in the area have been classified as mixed typic cryopsamments (Anon.
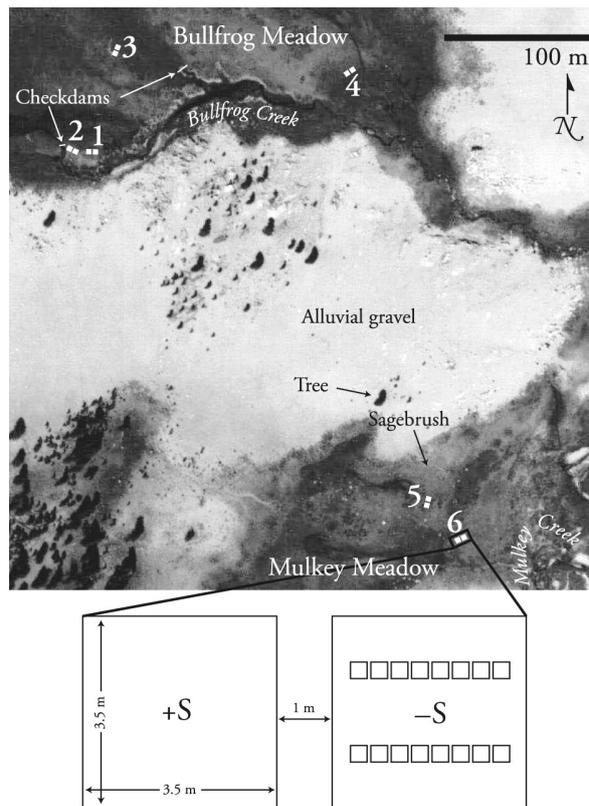

Fig. 1. Sagebrush removal experiment. Aerial photographs of the study site and diagram of plot design. We located six patches where sagebrush was actively invading herbaceous meadow and established blocks consisting of two adjacent 3.5 m × 3.5 m plots; we removed sagebrush from plots denoted –S. Outside of the highly reflective alluvial gravel, most of the darker patches are dense mats of wet herbaceous meadow while slightly lighter patches are drier sagebrush-invaded areas. The arrangement of quadrats used for percent cover measurements is shown in the –S plot.

2004b). We have found no evidence of recent fire in either meadow. With permission from the United States Forest Service, ranchers continue to graze cattle in Mulkey and Bullfrog Meadows at low stocking rates.

Mulkey and Bullfrog Meadows have both low-growing (< 20 cm) herbaceous patches and sagebrush-dominated areas. Relative to other meadows on the Kern Plateau, Mulkey Meadow is heavily encroached upon by sagebrush; Bullfrog Meadow, until recently, had less encroachment than most meadows (Swartz 2004). A diverse assemblage of herbs grow in the herbaceous patches (Berlow et al. 2003): there are more than 15 graminoid species including 12 grasses, several sedges, an abundant rush, *Juncus balticus*; and more than 50 forb species. These herbs are almost entirely native, with the only common nonnative species, *Taraxacum officinale*,

Table 1. Block characteristics: establishment date, depth to water table on 5 July 2003, percent sagebrush cover in +S plot, and geographic location of the six experimental blocks in the removal experiment. Locations are reported in UTM coordinates referenced to WGS-84. The water table in blocks 1 and 2 had descended below our 100 cm wells by an unknown amount.

Block	Date established	Water table depth (cm)	Percent sagebrush cover	Location
1	24.05.2001	138	21	11 S 0391257 E 4029242 N
2	24.05.2001	122	8	11 S 0391240 E 4029250 N
3	24.05.2001	115	5	11 S 0391280 E 4029320 N
4	25.05.2001	91	5	11 S 0391475 E 4029332 N
5	17.07.2002	>100	14	11 S 0391592 E 4028922 N
6	30.05.2003	>100	18	11 S 0391613 E 4028903 N

occupying <1% cover. For more site details, see Berlow et al. (2002).

Removal experiment

To determine the effects of newly colonizing sagebrush shrubs on soil resources and resident herbs, we experimentally removed young shrubs in recently colonized meadow areas (Fig. 1). We located our plots in areas where sagebrush shrubs were less than ca. 8 years old. The mean size ($\pm$ SD) of 2046 removed shrubs was 10.5 ± 6.9 cm in height and 7.0 ± 7.7 cm in canopy diameter; the modal height and canopy diameter were 7.0 cm and 2.3 cm. In comparison, adult sagebrush shrubs are typically 30-50 cm in height and 20-100 cm in canopy diameter. Because we observed considerable variation in water table depth, sagebrush cover, and other factors among these patches (Table 1), we blocked the experimental treatments over a range of encroachment conditions. Each experimental block contained two 3.5 m × 3.5 m plots where we removed all sagebrush individuals from one plot and left sagebrush shrubs intact in an adjacent plot (hereafter, –S and +S; see plot design diagram in Fig. 1). Blocks were placed in areas in which the two plots could be as similar as possible; the removal plot was selected randomly. On 24-25.05. 2001, we removed all sagebrush plants from the first four –S plots by clipping their above-ground biomass. To increase replication, two additional blocks were added: one on 17.07.2002 and the other on 30.05.2003.

We measured volumetric soil moisture in the plots using time domain reflectometry (TDR) probes (Environmental Sensors Inc., British Columbia). In 2001, we used a TDR probe that integrated soil moisture over the top 30 cm of the soil. In 2002 and 2003, we used multi-segmented TDR probes that measured 0-30 cm and 30-60 cm, and, in 2003, 60-90 cm. We made measurements at several dates during each season, though we were unable to make late season measurements in 2002 and 2003 because the hard dry soil prevented the insertion of the multi-segmented probe. At each measurement date, we took 3-6 subsamples per plot, which were then averaged prior to data analysis. For reference, volumetric soil

moisture varies from 0% when these soils are dry to ca. 60% when they are saturated. In addition to soil moisture measurements, we also measured depth to water table in each block using 2.54 cm diameter PVC piezometers.

We measured nitrogen mineralization and nitrification in the plots using laboratory incubations. On 12.06.2001 and 3 .08.2005, we collected six randomly selected 3 cm diameter, 15 cm deep soil cores in each plot. Measurements gathered from these cores were averaged within each plot prior to data analysis. Two cores were lost in 2001, for a total of 46, and five cores were lost in 2005, for a total of 67. The higher sample number in 2005 was due to the two additional blocks. Fresh soils were kept on ice until they could be extracted for mineral nitrogen in the laboratory at UC Berkeley in 2001 or at the University of Colorado Mountain Research Station in 2005. In the lab, samples were sieved through 2 mm mesh and a ca. 20 g subsample of each sample was extracted immediately with KCl. A second subsample was wetted to field capacity and incubated in the laboratory for two weeks. A third ca. 10 g subsample was immediately weighed and placed into a 100ºC drying oven for calculation of gravimetric moisture content. Soils were extracted using 2 M KCl in a 5:1 KCl to soil ratio. Samples were shaken on a rotary shaker for 45 minutes, filtered through pre-KCl-leached filter paper and then frozen until analysis. Thawed samples were analysed for ammonium and nitrate on a Lachat flow-injection autoanalyzer (Lachat, Milwaukee, WI, USA). Mineralization was calculated as final minus initial ammonium plus nitrate divided by 14 days. Nitrification was calculated as final minus initial nitrate divided by 14 days.

We measured herb abundance in the plots in mid-July of each season (except 2004) by visually estimating percent herb cover in 16 30 cm × 30 cm quadrats along two parallel transects in each plot (see sampling diagram in Fig. 1). We took the mean of these 16 estimates to represent each plot. Mid-July was chosen because it is the typical time of peak herbaceous biomass and physiological activity.

Data analysis

To estimate the effect of sagebrush removal on our response variables both throughout the course of the experiment and at individual timepoints, we subtracted the mean of the measurements in the control plots from the mean of the measurements in the removal plots. To quantify the uncertainty in these estimates, we fit linear mixed effects models predicting each of our measured variables as a function of the treatment, sampling time, and sampling block. This approach is similar to the standard ANOVA approach in that parameters are estimated using linear models; however, we report confidence intervals instead of *p*-values (see Tukey 1991; Johnson 1999; Hobbs & Hilborn 2006).

For measurements of herb cover and soil moisture, the uncertainties in the mean effect of sagebrush removal throughout the course of the experiment were estimated by modeling sampling year and time as crossed random effects (Pinheiro & Bates 2000). For the soil moisture model, we used the sampling year by time of season interaction as the random effect to account for the fact that multiple measurements were taken each season and separate models were fit for each of the three soil depths.

Thus, one random effect was fitted for each block and one for each year, but no effects were fitted for their nested combinations (Pinheiro & Bates 2000). To estimate the effect of sagebrush at individual timepoints, we modified the linear mixed effects models so that date was nested within block and the date by treatment interaction was assessed as a fixed factor in the absence of an overall treatment effect, thus creating a coefficient for the treatment on each sampling date.

In all models, the confidence intervals around the fixed treatment effects were used as estimates of uncertainty. The confidence intervals were calculated using the nlme package in R 2.4.0 (Pinheiro et al. 2006; R Core Development Team 2006). For each model, the validity of the model assumptions – that within group errors and random effect estimates are independent and identically normally distributed – were examined using the procedures described in Pinheiro & Bates (2000). In all cases, these assumptions were within acceptable limits except in the case of the mineralization and nitrification data. For these data, the variances were far from homogeneous between dates. Thus, each measurement date was examined separately using a paired *t*-test and a Bonferroni correction factor was applied across the two dates.
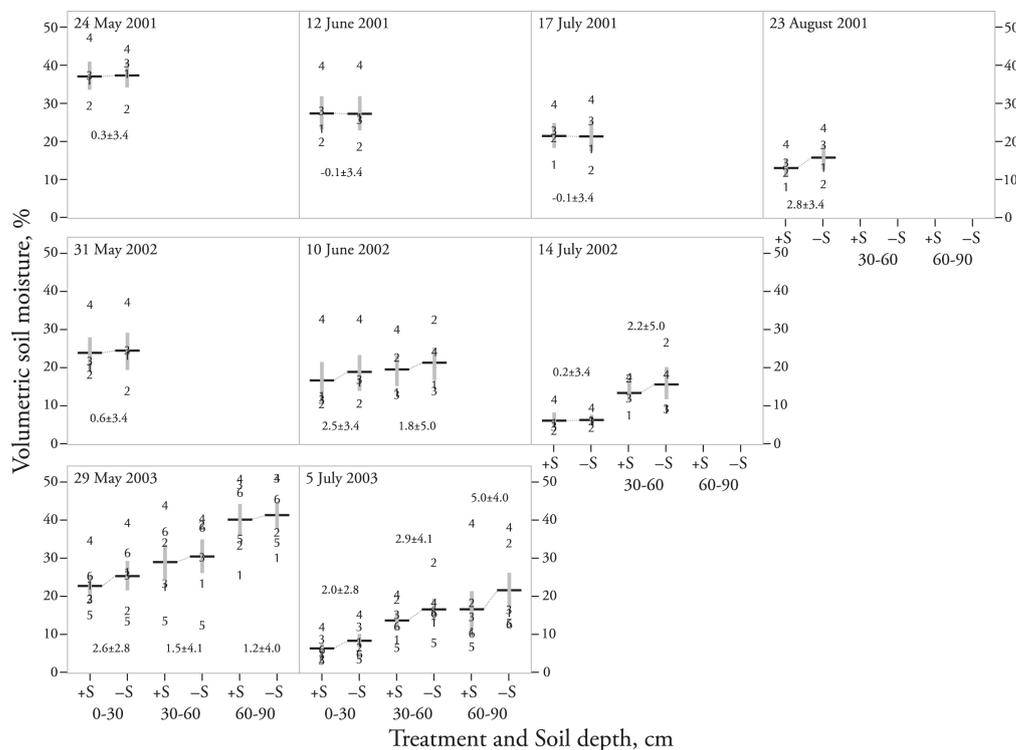

Fig. 2. Volumetric soil moisture, recorded using time domain reflectometry (TDR), in +S and −S plots throughout three summers. Flooded soil would show a volumetric soil moisture percentage of ca. 60%. For all measurement dates, volumetric soil moisture was measured at 0-30 cm soil depth. Additionally, in 2002 and 2003, a multi-segmented TDR probe allowed measurements at 30-60 cm, and in 2003, at 60-90 cm. Solid black lines indicate treatment means, gray bars are ±1 SE, and plotting symbol indicates paired plots (1-6). Each data point, representing the soil moisture for a particular date, treatment, depth, and block, is the average of three to six randomly chosen subsamples within the plot. The difference between treatment means (± 95% CI) is shown for each date and depth.

Results

Soil moisture

On average throughout the experiment, the difference in soil moisture due to removal was $1.3 \pm 2.0\%$ at 0-30 cm depth, $2.1 \pm 3.1\%$ at 30-60 cm depth and $3.1 \pm 5.8\%$ at 60-90 cm depth, with removal plots being wetter (Fig. 2; also, note that these are differences in percent volumetric soil moisture between treatments, not percent differences in percent volumetric soil moisture between treatments). While a ca. 2% difference in volumetric soil moisture would be small in the absolute amount of water it represents, a difference of this size would indicate that at the end of the season when the meadow is dry, –S plots would have ca. 20% more soil moisture than +S plots. During the first season, 2001, the mean difference between treatments was less than 0.5% until August, when it rose to $2.8 \pm 3.4\%$. At that time, three of the four blocks showed an increase of ca. 3% in shallow (0-30 cm) soil water in the removal plots and one of the four blocks, block 2, showed the opposite trend. During the following year, 2002, the largest difference was observed early in the season (June) when removal plots were $2.5 \pm 3.4\%$ higher. In the third year of treatment, 2003, both early and mid-season measurements showed that removal plots had ca. 2.5% more moisture.
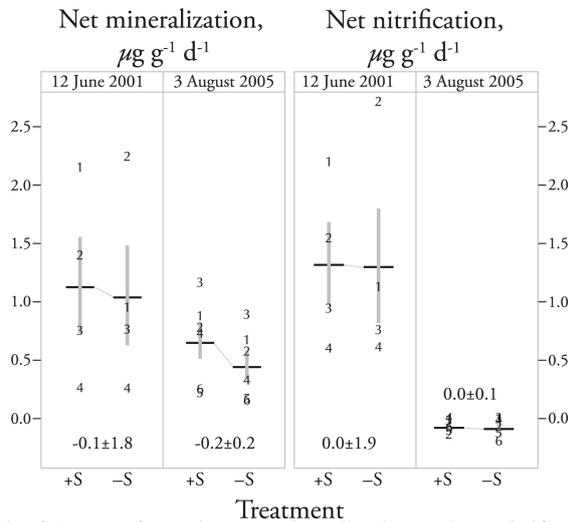
The deeper soil (60-90 cm) showed a larger difference, $5.0 \pm 4.0\%$, at mid-season (July).

Nitrogen mineralization and nitrification

On 12.06.2001, two weeks after the removal experiment was established, the differences between +S and –S treatments in net nitrogen mineralization and nitrification rates were uncertain (Fig. 3). The data were highly variable, spanning an order of magnitude (0.2-2.2 μg·g^{-1}·d^{-1} mineralized N) among the eight plots and showing large inconsistencies between paired plots in blocks 1 and 2 (Fig. 3). After four years of treatment, however, a consistent difference in nitrogen mineralization had developed between treatments. Mineralization rates were $30 \pm 20\%$ higher where young shrubs were present (Fig. 3). Though no treatment differences were observed in nitrification rates, there was a large discrepancy between the two years of data collection. In 2001, nearly all mineralized nitrogen was nitrified, whereas in 2005, net nitrification rates were negligible.

Herb abundance

On average, herb cover was $13.0 \pm 6.4\%$ higher in –S plots than +S plots throughout the experiment (Fig. 4; again, note that this is a difference in percent herb cover between treatments, not a percent difference in percent herb cover between treatments). Herb abundance was first measured six weeks after the experiment began. At that time, the percent cover of herbs varied from 37-98% among the eight plots in the experiment, and herb cover was already higher in –S plots by $12.9 \pm 9.8\%$. In 2002,
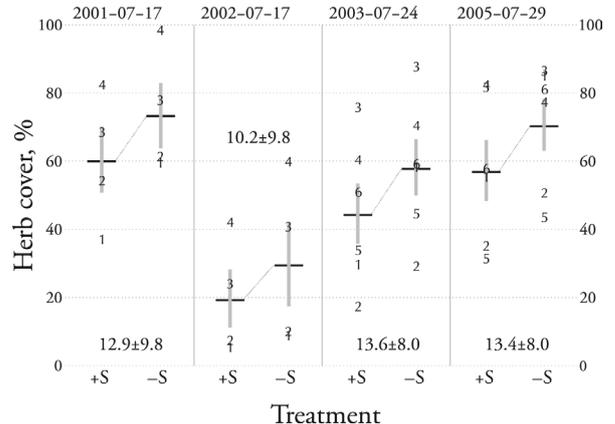

Fig. 3. Rates of net nitrogen mineralization and net nitrification in +S and –S plots on 12.06.2001 and 03.08.2005 reported per gram dry soil. Solid black lines indicate treatment means, gray bars are ±1 SE, and plotting symbols indicate paired plots (1-6). Each data point, representing the mineralization or nitrification for a particular date, treatment and block, is the average of four to six randomly chosen subsamples within the plot. The difference between treatment means (± 95% CI) is shown for each date.

Fig. 4. Percent herbaceous cover at peak herbaceous biomass in +S and –S plots over four growing seasons. Solid black lines indicate treatment means, gray bars are ± 1 SE, and plotting symbol indicates paired plots (1-6). Fig. 1 shows the arrangement of quadrats used to estimate the plot averages shown here. The difference between treatment means (± 95% CI) is shown for each date.

herb cover dropped drastically in all plots, likely as a response to low soil moisture as a result of a light snow pack that melted off early and a grasshopper irruption in the meadow. (In some areas, we estimated 50-100 grasshoppers per m^2.) During this herb decline in 2002, and after the herb recovery in 2003, herb cover continued to be higher is –S plots (by 10.2 ± 9.8% in 2002, 13.6 ± 8.0% in 2003, 13.4 ± 8.0% in 2005). An increase of ca. 13% cover is similar to the amount of sagebrush we removed, but the correlation between the percent cover of sagebrush removed in each block and the increase in percent cover of herbs in those blocks during the first year was poor (linear regression slope 95% CI = [–0.7, 1.1], $r^2 = 0.08$, $n = 6$).

Discussion

Effects of sagebrush on soil resources and herb cover

Our results show that encroaching sagebrush shrubs have substantial effects on soil resources and resident herb cover even during the early stages of encroachment. The most dramatic effects we observed were the rapid increase in herb cover and the decrease in N-mineralization with the removal of encroaching shrubs. Our data on soil moisture are less conclusive: while they show that sagebrush removal had a small absolute effect on soil moisture at all measured time points, we cannot rule out the possibility that proportional change in soil moisture was enough to affect herb growth or be otherwise ecologically relevant.

The reduction in herb cover that we observed constitutes a ca. 50% change in percent cover between treatments. As sagebrush seedlings grow into adults, they will likely displace more resident herbs. Herb increases in response to removing adult woody plants have been documented in this (Berlow et al. 2003) and other systems (e.g., Harrington & Johns 1990; Köchy & Wilson 2000; Lett & Knapp 2003), but this study is perhaps the first to document that the negative effects of shrubs on herbs may begin very early in the encroachment process. While the ca. 13% reduction in herb cover is similar to the amount of sagebrush seedling cover removed, the absence of correlation between the amount of sagebrush removed and the amount of herb increase across plots suggests that local resource conditions may be important in determining the magnitude of the exchange between shrub and herb cover.

The lack of a strong effect of shrub removal on soil moisture may be due to the rapid herb response to the removal of sagebrush. The rapid herb response could have resulted in a compensatory increase in herb water use for water that otherwise would have been transpired by sagebrush. This is consistent with the predictions of Chapin et al. (1996) who suggested that when invaders overlap strongly with residents in their use of a limiting resource (in our study, shallow soil moisture), strong ecosystem impacts will not occur because of compensatory responses when the invader or resident is removed.

The increase in N-mineralization attributable to encroaching sagebrush is broadly consistent with studies of shrub encroachment in other systems (e.g. Schlesinger et al. 1996; Hibbard et al. 2001). Again, our study emphasizes that these changes can occur while shrubs are still colonizing a site and are well below their adult size. Although our study did not examine the mechanism behind this change, other studies that focus specifically on nutrient cycling have suggested factors such as higher fine root turnover under shrubs, altered litter chemistry due to shrub inputs, and changes in the microbial community under shrubs (Schlesinger et al. 1996; Ehrenfeld 2003; Hawkes et al. 2005). The higher rates of N mineralization that we observed may alleviate the effects of nutrient limitation for both encroaching sagebrush and resident herbs.

Although our study does not specifically investigate the cause of the reduction in herb cover, the combined evidence from this study and others in our system point to competition for water as the most likely mechanism. Measurements of the oxygen stable isotopes in soil, sagebrush, and herb water show that there is substantial overlap in the depth of water acquisition by young sagebrush and some meadow herbs, thus allowing for competition (Darrouzet-Nardi et al. 2006). A watering experiment in Mulkey Meadow showed that adult sagebrush shrubs respond positively to added soil moisture (Berlow et al. 2003). In that experiment, shortly after the watering began, sagebrush took up shallow water, preventing herbs from using the extra water to increase their biomass. Several other possible mechanisms seem much less likely. Competition for light has been demonstrated in other examples of shrub encroachment (e.g., Lett & Knapp 2003), but the relatively small size and open canopies of sagebrush shrubs in this study as well as examinations of carbon isotopes in herbs growing under and away from sagebrush canopies (A. Darrouzet-Nardi and N. Aslami unpubl. data) suggest that light competition is less important than below-ground competition. Of the below-ground factors, nitrogen mineralization has been shown to *increase* with encroachment in this study, which makes it unlikely that sagebrush is competitively reducing herbs by nitrogen pre-emption. Finally, this study has shown that the difference in soil moisture caused by sagebrush removal was not large, allowing for the possibility of a compensatory reduction in herbs with sagebrush encroachment.

Implications for shrub encroachment

The rapid reduction in herb cover may be an important positive feedback to shrub encroachment in our study system. Berlow et al. (2002) showed that for sagebrush seeds to germinate and establish, they need bare patches of meadow soil. Thus, sagebrush individuals may be facilitating the future establishment of other sagebrush plants by reducing herb cover during the early stages of encroachment. This feedback mechanism could be particularly important in allowing sagebrush to form nearly monospecific stands once it gains a foothold. The development of such a feedback may still require a trigger such as groundwater decline or climate change to initiate encroachment. This feedback between woody plant establishment and herbaceous dieback has been suggested in at least one other system, a mountain-top meadow in Oregon (Magee & Antos 1992). Thus, this type of feedback might be a more general phenomenon. We would predict it to be most relevant in systems such as ours and the Oregon meadow that have dense mats of herbs that prevent woody plants from establishing. However, even in the drier savannas of Texas, competition from herbs has been shown to slow, if not completely prevent, woody plant establishment (Jurena & Archer 2003). In other systems such as African savannas, fire may be the more important factor preventing woody shrub establishment (Roques et al. 2001), thus making the type of competitive feedback we observed in our system less important.

Our study results are encouraging for restoration efforts because the magnitude of the effect on meadow soil moisture that we observed was small within the first 8-10 years of invasion, and because meadow herbs increased quickly following the removal of young sagebrush. Thus, these newly encroached-upon meadow patches are likely to exhibit high potential for recovery to an herb-dominated state provided that groundwater decline has not already dried the soil. A restoration experiment in riparian areas of the Great Basin (Nevada, USA) in which fire was used to remove *Artemisia tridentata* shrubs supports this conclusion by showing that restoration worked best when shrubs were removed and when water tables were still high (Chambers & Linnerooth 2001; Wright & Chambers 2002). Together, the results of our study and others suggest that ongoing restoration efforts in the meadows of the Sierra Nevada and in other riparian zones of the semi-arid West should not only prevent further groundwater decline, but should also include targeted shrub removal in newly encroached upon areas, particularly areas where the water table is still high.

References

Anon. 2004a. *Precipitation / Snow information*. California Department of Water Resources. http://cdec.water.ca.gov/snow_rain.html *Accessed* February 21, 2004.

Anon. 2004b. *National Soil Survey characterization data: Pedon Number 91P1142*. National Soil Survey Center, USDA-NRCS, Lincoln, NE, US.

Bauer, K.M., Berlow, E.L. & D'Antonio, C.M. 2002. The relationship between climate and Rothrock sagebrush colonization patterns. *Journal of Range Management* 55: 620-625.

Berlow, E.L., D'Antonio, C.M. & Reynolds, S.A. 2002. Shrub expansion in montane meadows: The interaction of local-scale disturbance and site aridity. *Ecological Applications* 12: 1103-1118.

Berlow, E.L., D'Antonio, C.M. & Swartz, H. 2003. Response of herbs to shrub removal across natural and experimental variation in soil moisture. *Ecological Applications* 13: 1375-1387.

Chambers, J.C. & Linnerooth, A.R. 2001. Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts - the establishment component. *Applied Vegetation Science* 4: 157-166.

Chapin, F.S. & Shaver, G.R. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77: 822-840.

D'Antonio, C.M. 2000. Fire, plant invasions, and global changes. In: Mooney, H.A. & Hobbs, R.J. (eds.) *Invasive species in a changing world*, pp. 55-64. Island Press, Washington, DC, US.

Darrouzet-Nardi, A., D'Antonio, C.M. & Dawson, T.E. 2006. Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow. *Plant and Soil* 285: 31-43.

Dull, R.A. 1999. Palynological evidence for 19th century grazing-induced vegetation change in the southern Sierra Nevada, California, U.S.A. *Journal of Biogeography* 26: 899-912.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503-523.

Harrington, G.N. & Johns, G.G. 1990. Herbaceous biomass in a Eucalyptus-savanna woodland after removing trees and or shrubs. *Journal of Applied Ecology* 27: 775-787.

Hawkes, C.V., Wren, I.F., Herman, D.J. & Firestone, M.K. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters* 8: 976-985.

Hibbard, K.A., Archer, S., Schimel, D.S. & Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* 82: 1999-2011.

Hobbs, N.T. & Hilborn, R. 2006. Alternatives to statistical hypothesis testing in ecology: A guide to self teaching. *Ecological Applications* 16: 5-19.

Huenneke, L.F., Anderson, J.P., Remmenga, M. & Schlesinger, W.H. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* 8: 247-264.

Johnson, D.H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63: 763-772.

Jurena, P.N. & Archer, S. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84: 907-919.

Köchy, M. & Wilson, S.D. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91: 385-395.

Lett, M.S. & Knapp, A.K. 2003. Consequences of shrub expansion in mesic grassland: Resource alterations and graminoid responses. *Journal of Vegetation Science* 14: 487-496.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 270: 775-781.

Magee, T.K. & Antos, J.A. 1992. Tree invasion into a mountaintop meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science* 3: 485-494.

Muir, J. 1911. *My first summer in the Sierra*. Houghton Mifflin Company, Boston, MA, US.

Pinheiro, J.C. & Bates, D.M. 2000. *Mixed-effects models in S and S-PLUS*. Springer, New York, NY, US.

Pinheiro, J.C., Bates, D.M., DebRoy, S. & Sarkar, D. 2006. *NLME: Linear and nonlinear mixed effects models*. R package version 3.1-77.

R Development Core Team 2006. *R 2.4.0: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.

Roques, K.G., O'Connor, T.G. & Watkinson, A.R. 2001. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* 38: 268-280.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364-374.

Shultz, L.M. 1983. Origin and distribution of *Artemisia rothrockii* Asteraceae Anthemideae. *American Journal of Botany* 70: 129.

Stromberg, J.C., Tiller, R. & Richter, B. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: The San Pedro, Arizona. *Ecological Applications* 6: 113-131.

Suding, K.N., Gross, K.L. & Houseman, G.R. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19: 46-53.

Swartz, H. 2004. Patterns of sagebrush (*Artemisia rothrockii*) expansion in montane meadows of the Kern Plateau, Southeastern Sierra Nevada. Ms Thesis, University of California, Berkeley, Berkeley, CA, US.

Tukey, J.W. 1991. The philosophy of multiple comparisons. *Statistical Science* 6: 100-116.

Wright, J.M. & Chambers, J.C. 2002. Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts – above-ground vegetation response. *Applied Vegetation Science* 5: 237-246.